OCCASIONAL PAPERS
THE MUSEUM
TEXAS TECH UNIVERSITY

NUMBER 147 5 MARCH 1992

EVOLUTIONARY SIGNIFICANCE OF THE ENAMEL CUSP PATTERNS OF MODERN GEOMYID PREMOLARS

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Cheekteeth of the superfamily Geomyoidea range from brachyodont to strongly hypsodont. Cusps form on the enamel caps at the occlusal ends of the developing teeth while deep in their alveoli. The cusp pattern is confined to the enamel cap and, especially in low-cusped, strongly hypsodont teeth, is lost as soon as the enamel cap is worn away.

The cheekteeth of modern pocket gophers, Geomyidae, wear swiftly and the enamel cap and its cusp pattern are present only in young individuals. In contrast, some mammals with strongly hypsodont cheekteeth (rabbits, horses, voles, and elephants, for example) have cusps surrounded by enamel walls that grow from the tooth germ as the occlusal end is worn away. Such cusps are visible in occlusal view at almost all stages of tooth wear. Their patterns furnish definitive characters that may identify and determine relationships among families, genera, and even species. Cusp patterns of modern geomyids may be equally important, but rarely have been utilized or adequately described or figured.

Although Merriam (1895) figured the enamel cap of a young *Orthogeomys* he did not attempt to interpret the cusp pattern. Rensberger (1971) briefly described cusp patterns of *Thomomys* but did not figure them. He also utilized Merriam's figures of *Orthogeomys* in comparisons with teeth of *Entoptychus*. We are aware of no other published descriptions of the enamel cap of the premolars of modern geomyids. The enamel cap of modern genera is complicated and highly derived. However, SEM micrographs indicate the cusp patterns in modern gophers are as characteristic as those of other geomyoids.

Materials and Methods

Merriam (1895) could find but four specimens, three *Geomys* and one *Heterogeomys* (= *Orthogeomys*) of exceptionally young pocket gophers in the large collections of the U. S. Biological Surveys. The situation is not greatly different today. Young mammals are rare in collections (for discussion of collecting biases see Dalquest and Carpenter, 1986, and Stangl and Jones, 1987). We suspect that the scarcity of young pocket gophers in collections may result, in part, from confinement of immature gophers to the nest area where they would not be taken in the traps usually used for capturing these animals. We found seven suitable young specimens of *Geomys* in the collections at Midwestern State University and Texas Tech University, but none of other genera. Young *Thomomys* may be more common in collections than *Geomys*. James C. Patton, Museum of Vertebrate Zoology, University of California at Berkeley, loaned us 10 specimens with the deciduous premolars still partly covering the crowns of the permanent premolars. However, the only young *Cratogeomys* we could find (mentioned by Hollander, 1990) was made available by C. S. Thaler, New Mexico State University. No young *Zygogeomys* have been examined. We have relied on Merriam's (1895) figures of the premolars of *Orthogeomys*.

Pocket gopher teeth lie in their alveoli at different angles to each other (Merriam, 1895). The plane of the occlusal surface of a worn upper premolar (P4) may be at almost a 45° angle to the long axis of the tooth, whereas the slightly curved lower premolar (p4) is almost upright in the jaw. Consequently, an occlusal view of P4 is highly distorted from the cross-sectional view of the same tooth. In the micrographs and drawings that follow, views of P4s are those that best illustrate features discussed and are not necessarily views perpendicular to occlusal surfaces.

Different workers have applied different names to the cusps of geomyoid premolars. This results, in large part, from use of molar cusp terminology for premolars. However, premolar cusps are not homologous to the cusps of molars. Cusp nomenclature in the complicated enamel caps (greatly modified from the primitive premolar pattern) of modern pocket gophers is especially difficult. Because the cusps of premolars are not homologous to those of molars there can be no "correct" terminology. We utilize priority in cusp terminology and follow Wood (1935, 1936) whenever possible (Fig. 1). Some alternatives that

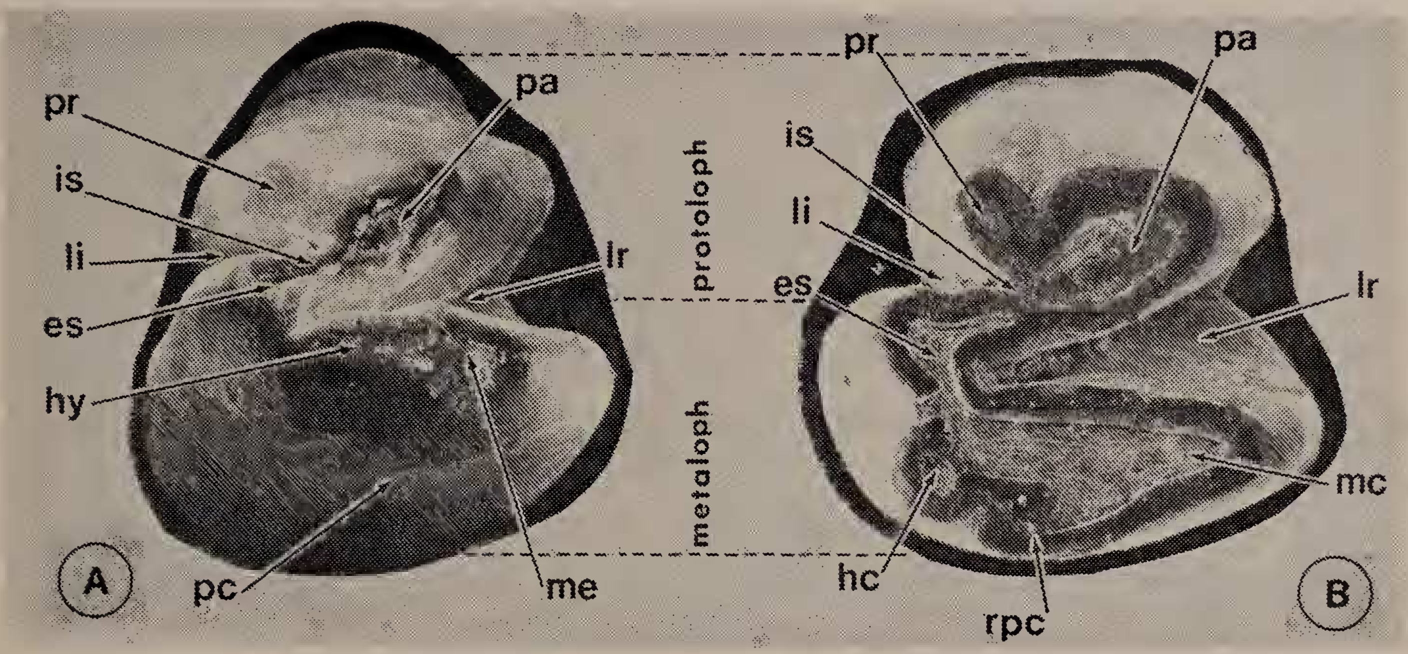

FIG. 1.—Upper premolars of *Pliosaccomys higginsensis*, Higgins local fauna, early Hemphillian land mammal age, mid-Miocene; A, enamel cap almost unworn; B, enamel cap lightly worn. Abbreviations: pr, protocone; pa, paracone; lr, labial re-entrant; me, metacone; pc, posterior cingulum; hy, hypocone; rpc, remnant of posterior cingulum; es, entostyle; li, lingual re-entrant; is, isthmus.

have been used by other workers are given in parentheses following first use of cusp names. We also use "isthmus" for the anteroposterior connection of protoloph to metaloph and protolophid to metalophid.

Modern pocket gophers and their extinct relatives have been ranked as both a family and a subfamily. We follow Wahlert (1985) as the most recent revisor and consider the Geomyidae a full family. Drawings were made by Russell Pfau.

Enamel Cap Pattern in Miocene Geomyids

The primitive cusp pattern of the enamel cap of the upper premolar of geomyoid rodents may have included a triangular protoloph consisting of anterior cingulum (anterocone), lingual protocone, and labial paracone, separated from the metaloph by a transverse central valley. The metaloph probably included a lingual entostyle (hypostyle), medial hypocone, and labial metacone. As early as the medial Oligocene, *Heliscomys vetus* had lost anterior cingulum and paracone (Korth, 1990). (Citations in this section are to publications where features mentioned are well illustrated.) The resultant, simplified pattern of protoloph consisting of protocone alone, and metaloph of entostyle, hypocone, and metacone, arranged in a line or arc, is common in Tertiary geomyoids and persists today in *Perognathus*. In some geomyoids, the protoloph may be broadened by addition of accessory cusps (protostyles). A connecting isthmus usually forms between protoloph and metaloph, at least in late stages of tooth wear, and in the enamel cap of unerupted premolars of hypsodont taxa. The position of the isthmus in strongly hypsodont premolars is an important diagnostic character.

The cusp pattern of the P4 enamel cap of *Dikkomys*, the early Miocene ancestor of the geomyids, is unknown. *Parapliosaccomys* Shotwell (Barstovian through Clarendonian land mammal ages) and *Pliosaccomys* Wilson (Clarendonian through early Hemphillian) are definitely ancestral geomyids. In most geomyoids, the isthmus connecting protoloph to metaloph extends anteroposteriorly along the lingual, central, or labial axes of the P4, but in *Parapliosaccomys* and *Pliosaccomys* it passes obliquely from the entostyle to the labial side of the protocone, or to a cuspule labial to the protocone. With slight wear the protoloph, isthmus, and metaloph form a Z-pattern rather than the eight-pattern of other geomyoids (exclusive of the Entoptychidae, all of which have a C-pattern). In the Z-pattern, the lingual re-entrant lies in advance of the labial re-entrant rather than opposite, as in other geomyoids. Only in later stages of wear does the eight-pattern appear. When unworn, the protoloph appears anteroposteriorly compressed but transversely broad. Accessory styles, some elongated to small lophs, may appear but are shallow and swiftly worn away. The anteroposteriorly compressed metaloph bears the usual three cusps: entostyle, hypocone, and metacone. The isthmus extends from the entostyle but is not the entostyle itself, for this cusp remains distinct. The Z-pattern of *Parapliosaccomys* and *Pliosaccomys* is considered to be a synapomorphic character retained from a common ancestor. In other respects, the two genera are quite different in several dental characters.

Shotwell (1967: fig. 23A) figured the almost unworn P4 of *Parapliosaccomys oregonensis* with a thin but broad posterior cingulum across the posterior margin (Fig. 2) but noted that it is "short lived." The posterior cingulum of *Pliosaccomys* has not been described but (Fig. 1A) is, like that of *Parapliosaccomys*, a sharp-edged crest bordering the tooth posteriorly and, with slight wear, incorporated into the hypocone.

The enamel cap of the lower premolar of geomyoids usually has four major cusps: protolophid formed by lingual protoconid; labial mesoconid; metalophid formed of lingual metaconid (entoconid); and labial hypoconid. Protolophid and metalophid are connected medially to form an X-pattern (Wood, 1935).

Early wear stages of the p4 of *Parapliosaccomys* are figured by Shotwell (1967). The protolophid is narrow and rounded; the metalophid is broader and antero-posteriorly compressed. In early wear stages, the

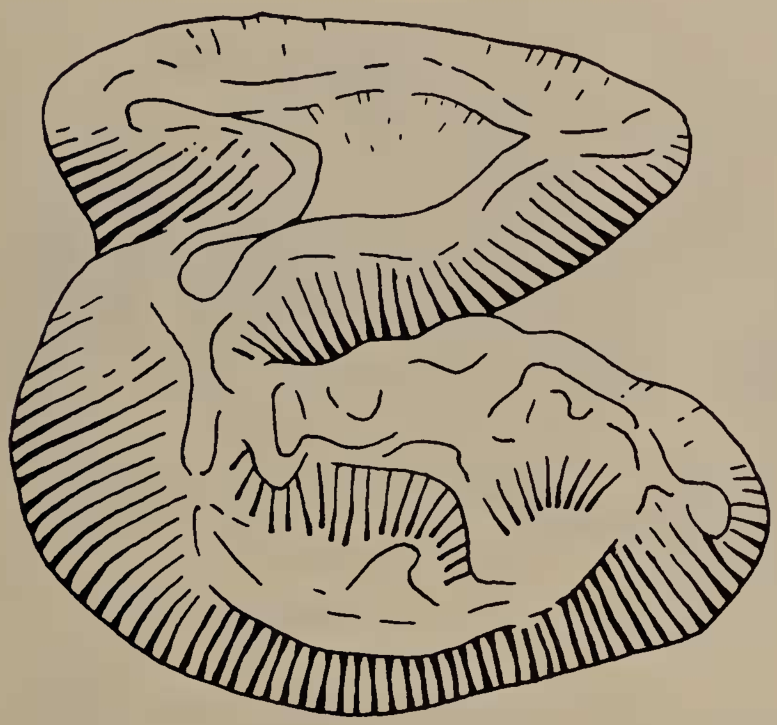

FIG. 2.—Upper premolar of *Parapliosaccomys oregonensis*, McKay Reservoir local fauna, Oregon, Hemphillian land mammal age, mid-Miocene, after Shotwell, 1967. For details see Figure 1.

protolophid has three cuspids or short lophids: protoconid, medial anteroconid, and mesoconid. Tiny accessory cuspids (protostylids) may be present as well. The metalophid is more elevated than the protolophid and comes into wear earlier. The cusps usually are obliterated when the cusps of the protolophid are but lightly worn. Presumably there are two cusps: metaconid and hypoconid. This differential wear destroys the X-pattern. With moderate wear the protolophid takes, briefly, a trefoil pattern (Wilson, 1936) followed by the eight-pattern of the mature geomyid p4.

An unerupted p4 of *Pliosaccomys* was figured by James (1963). Protoconid and mesoconid are prominent bulges but the anteroconid is a comparatively small intervening cusp. The large metalophid, with metaconid and hypoconid, is prominent, and a small isthmus appears to be a continuation of the anteroconid. Wilson (1936) has figured several lightly worn p4s of *Pliosaccomys*. The three cusps of the unworn p4 protolophid are relatively larger (Fig. 3), especially the anteroconid, than in the specimen figured by James (1963) but the pattern is the same. A short isthmus and two-cusped metalophid are present. A small cuspid also may be present between metaconid and hypoconid where the isthmus joins the metalophid. Unlike *Parapliosaccomys*, the metalophid of p4 does not seem to wear away before the cusps of the protolophid are destroyed.

Parapliosaccomys and *Pliosaccomys* share the Z-pattern of the upper premolars and the Z-pattern is present, in modified form, in modern pocket gopher genera. Chronologically, either or both of the Miocene gophers could be ancestral to modern genera. Therefore, the enamel cap patterns of modern pocket gophers can be interpreted from the enamel cap patterns of the extinct taxa.

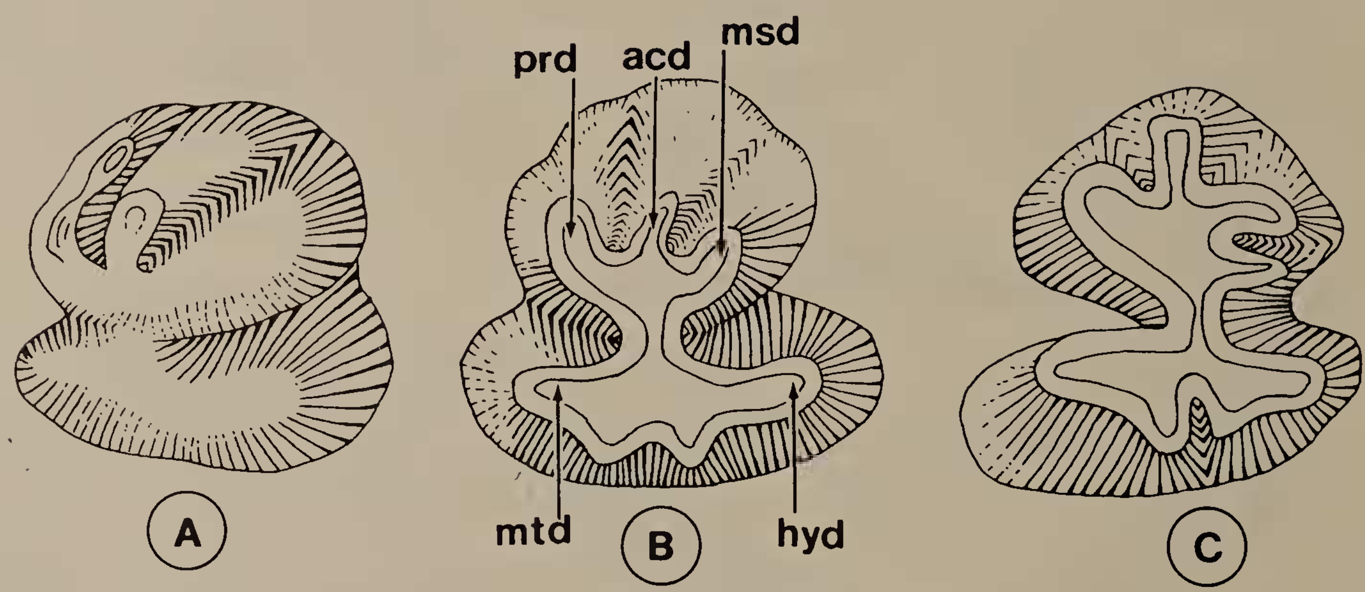

Fig. 3.—Lower premolars of *Pliosaccomys dubius*, Smiths Valley local fauna, Nevada, Hemphillian land mammal age, mid-Miocene, after Wilson, 1936. A, enamel cap unworn; B, enamel cap lightly worn; C, enamel cap lightly worn. Clockwise from upper left, prd, protoconid; acd, anteroconid; msd, mesoconid; hyd, hypoconid; mtd, metaconid.

Enamel Cap Patterns of Modern Geomyids

Upper Premolars

Considering first the upper premolars, the cusp patterns of modern pocket gophers are complicated and specialized but readily derived from those of *Parapliosaccomys* and *Pliosaccomys* (Fig. 4). The cusps of the major lophs and lophids tend to fuse and form thin crests. The oblique isthmus becomes exaggerated and a large posterior cingulum forms a transverse loph almost as prominent as the major lophs. Individual variation was studied in teeth of the extinct *Geomys* (*Nerterogeomys*) *minor* Gidley, from the Beck Ranch local fauna, Blancan land mammal age, of Texas. Nine randomly chosen, unerupted or scarcely worn, P4s were figured under a camera lucida (Fig. 5). Only minor variation is apparent. All P4s resemble the P4 of a modern *Geomys bursarius* except in minor details. None of the variations approach the magnitude of the differences in pattern separating the *Geomys* cusp pattern from those of *Thomomys*, *Cratogeomys*, and *Orthogeomys*. It is assumed that the amount of individual variation in the P4s of these genera is like that found in *Geomys*. Three *Thomomys* P4s examined all resemble the tooth shown in Fig. 4A. However, only one *Cratogeomys* was available, and for *Orthogeomys* we had only Merriam's (1895) figures.

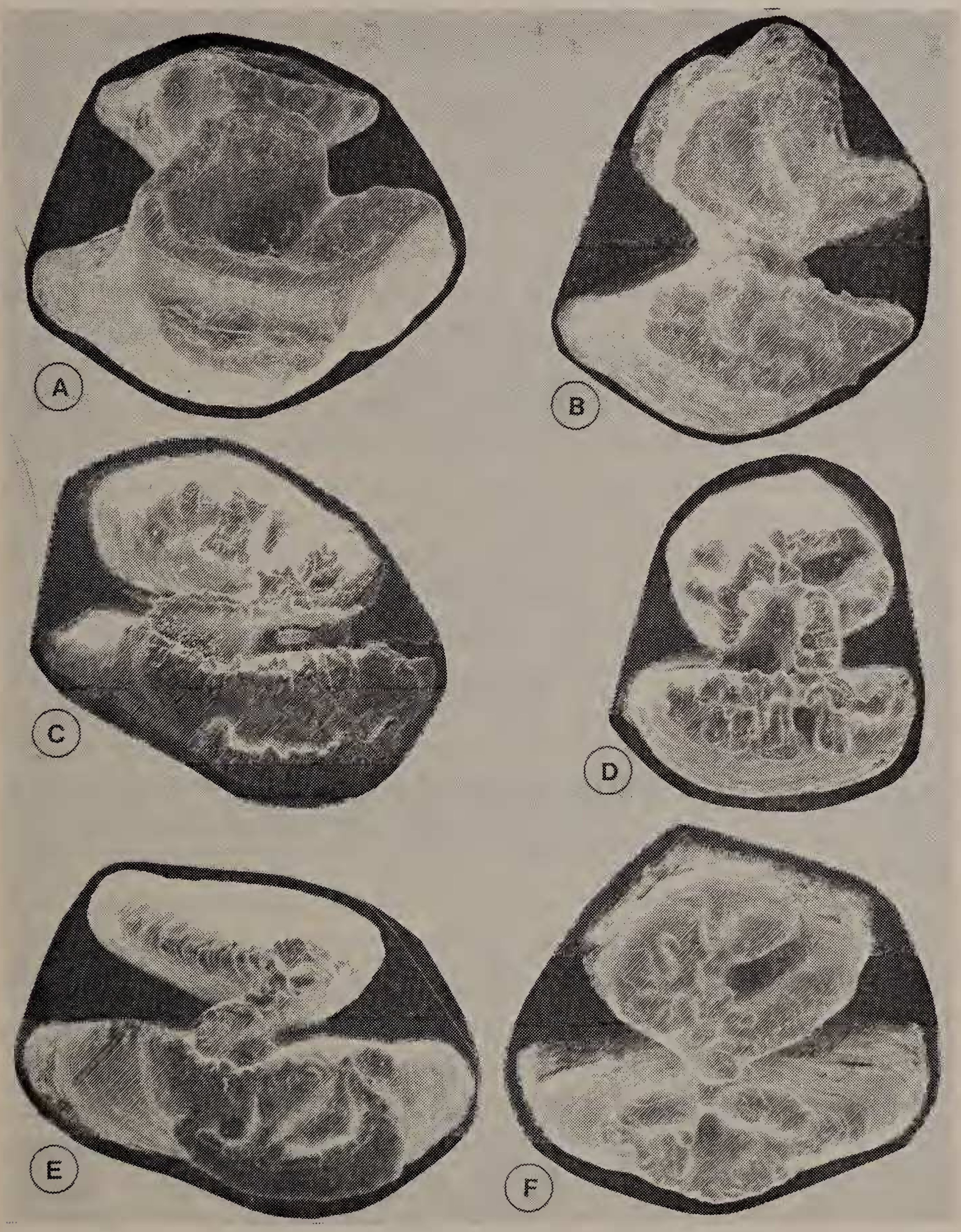

FIG. 4.—Enamel cap patterns of unerupted upper premolars (left) and lower premolars (right) of three genera of modern geomyids. A, *Thomomys bottae*, with deep, broad labial re-entrant and crests without denticulation. C, *Geomys bursarius* with oval protoloph, narrow, compressed labial re-entrant, and denticulated crests. E, *Cratogeomys castanops* with single-cusped protoloph, abbreviated isthmus and labial re-entrant, and denticulated crests. B, *Thomomys bottae* with shallow re-entrant between mesoconid and anteroconid and lacking denticulation on crests. D, *Geomys bursarius* with denticulated crests and elongated isthmus. F, *Cratogeomys castanops* with denticulated crests, compressed metalophid and abbreviated isthmus. For details see Figure 1.

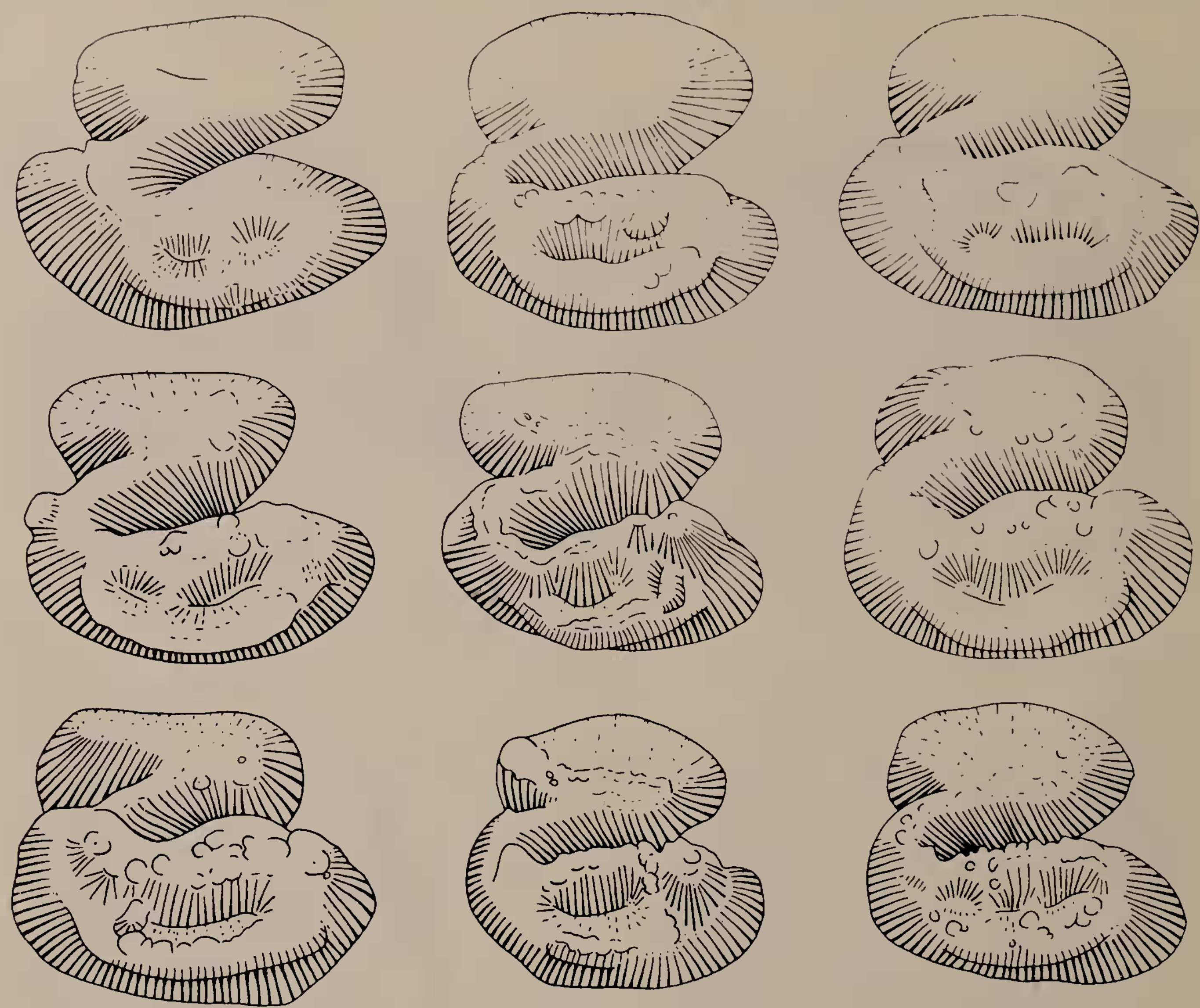

FIG. 5.—Camera lucida drawings of nine randomly chosen upper right premolars of *Geomys* (*Nerterogeomys*) cf. *minor* from the Beck Ranch local fauna, Blancan land mammal age, Texas, showing limited amount of individual variation in enamel cap pattern of P4 in this genus.

Rensberger (1971) noted the basic structure of the enamel cap of P4 in *Thomomys*. The protoloph is anteroposteriorly compressed, almost flat anteriorly. The isthmus is connected to the protocone anteriorly and the smaller paracone is distinct labially. The isthmus continues labially and doubtless connects to the paracone with slight wear. Posteriorly the crest of the metaloph begins at a swollen metacone and passes lingually across the metaloph, then turns anterolabially to outline a large, deep posteriorly placed labial re-entrant (fossette of Rensberger, 1971). The fossette is partly closed on the labial side by the metacone posteriorly and the paracone anteriorly. Hypocone and entostyle are not apparent as separate cusps and must be incorporated into the metaloph crest. A prominent posterior cingulum passes transversely across the posterior margin of the enamel cap, separated from the metaloph by a well-marked valley. The crests of P4 (protoloph, isthmus, metaloph, and posterior cingulum) are smooth-edged, not denticulated, as are the crests of other geomyid genera examined.

The protoloph of P4 of *Geomys* is broader than that of *Thomomys* and oval in shape, rounded anteriorly. Cusps are not distinct on the protoloph but a deep pit seems to set off the protocone from the paracone. A swollen area at the labial extremity of the metaloph crest may or may not be present. If present it may be the remnant of the metacone. No distinct cusps are present on the thin, strongly denticulated metaloph crest that passes lingually across the breadth of the tooth, and turns abruptly backward to form a narrow labial re-entrant and join with the labial extremity of the protoloph. A denticulated posterior cingulum is similar in size and position to that of *Thomomys*.

The P4 of *Cratogeomys* is even more specialized than that of *Geomys*. The protoloph is a single compressed, denticulated, and pointed crest presumably consisting of protocone alone. The isthmus is short, denticulated, oblique in position, and not completely connected to the metaloph at the upper surface. The metaloph is a denticulated crest with no defined cusps. Lingual and labial valleys are narrow. The posterior cingulum is heavy and seems to connect labially to the metaloph. The denticulated crests resemble those on the P4 of *Geomys*, but details of the cusp pattern of *Cratogeomys* indicate that this genus is almost as different from *Geomys* as *Geomys* is from *Thomomys*.

Understanding of the enamel cap of P4 of *Orthogeomys* is based on Merriam's (1895) figure, which, unfortunately, is a somewhat oblique view, and some details are not clear. The protoloph is divided into, presumably, protocone and paracone. The isthmus is shown as thin and low. Cusps are apparent on the broad metaloph. A strong posterior cingulum is separated from the metaloph by a valley. SEM micrographs are needed for detailed comparisons but resemblance to the P4 of *Geomys* is suggested.

Lower Premolars

Rensberger (1971) noted individual variation in the lower premolars of *Thomomys*, but this may be due partly to differences in wear. The few p4s of *Thomomys* that we examined seemed to be quite consistent in pattern. Certainly this is true of those of *Geomys*.

The enamel cap pattern of p4 of *Thomomys* differs strongly from that of *Geomys* and *Cratogeomys*. In *Thomomys*, the protolophid is not symmetrical. The protoconid is a broad, triangular cusp, set off from the anteroconid by a shallow re-entrant. The anteroconid is not distinct except as an anterior projection. The mesoconid is also not prominent and the labial side of the protolophid is truncated, not projecting laterally as does the protoconid. The isthmus is broad and short. The metalophid is compressed, with metaconid and hypoconid tapering to pointed ends. As in the P4, the crests are not denticulated.

The *Geomys* p4 is almost bilaterally symmetrical. The protolophid is rounded, and the protoconid is set off from the anteroconid by a deep pit or fossettid rather than a broad re-entrant. There is no obvious or consistent separation of anteroconid and mesoconid. The denticulated isthmus is moderately long and comparatively slender. The metalophid is compressed, broad, and heavily denticulated. A deep fossettid appears to separate metaconid from hypoconid.

The p4 of *Cratogeomys* resembles that of *Geomys* but differs in details. It is bilaterally symmetrical (X-pattern). The protolophid is rounded, the protoconid separated from the rest of the protolophid by a deep fossettid. A small, rounded anterior cuspule may be the anteroconid, or there may be no true separation of anteroconid from paraconid. The isthmus is quite short, a mere connection of the major lophids. The metalophid is compressed with metaconid and hypoconid separated by a deep fossettid.

Merriam's (1895) figure of the p4 of *Orthogeomys* is an occlusal view and permits ready comparison with teeth of *Geomys* and *Cratogeomys*. The p4 is almost perfectly symmetrical. Three distinct cusps: protoconid, anteroconid, and paraconid, are present on the protolophid. The isthmus is short, like that of *Cratogeomys*, and denticulated. Metaconid and hypoconid are equal in size, forming the compressed metalophid. This modified X-pattern forms almost a perfect H. A major difference between the p4 of *Orthogeomys* and those of *Geomys* and *Cratogeomys* is the compressed, flattened rather than rounded, protoloph of the former.

Relationships in the Geomyidae

Wood (1936) suggested that the early Miocene *Dikkomys matthewi* represented an early stage in the evolution of the Geomyidae. The teeth figured by Wood do not belong to the Entoptychidae, but no P4s were described. Galbreath (1948) figured a lower jaw of *Dikkomys* from South Dakota. Black (1961) figured the p4 and m1 of a new species, *Dikkomys woodi*, from Meagher County, Montana. Black considered the Deep River formation, where the specimen was collected, to be from the Hemmingfordian land mammal age but Tedford *et al.* (1987) listed the Deep River formation as Hemmingfordian and Barstovian. Chronologically, the range of *Dikkomys* approaches the early records of *Parapliosaccomys* (Barstovian through Clarendonian). All of the above workers, as well as Russell (1968), seemed to consider later geomyids to be descendent from *Dikkomys*. Unfortunately, no upper premolars of a species of *Dikkomys* seem to have been described and it is not known if the enamel cap of P4 in this genus had the Z-pattern.

Mojavemys Lindsay, from the Barstovian of California, was placed by Lindsay (1972) in the Geomyinae (=Geomyidae as used here). Enamel cap patterns of two species are figured. The P4s show a simple pattern with a single-cusped protoloph connected to the metaloph along the lingual margin, and not the oblique isthmus here considered characteristic of the Geomyidae.

The family Geomyidae includes, in addition to *Dikkomys*, the extinct *Parapliosaccomys* Shotwell, *Pliosaccomys* Wilson, *Progeomys* Dalquest, *Pliogeomys* Hibbard, all of Hemphillian age or older, and the extant *Thomomys* Wied-Neuwied, *Geomys* Rafinesque, *Zygogeomys* Merriam, *Cratogeomys* Merriam, and *Orthogeomys* Merriam. This encompasses most of the genera included by Russell (1968) in the subfamily Geomyinae.

Anatomical characters that have been used to classify pocket gophers include skull morphology (Wahlert, 1985), ultrastructure of teeth (Buzas-Stevens and Dalquest, 1991), morphology of molars (Russell, 1968), grooves of upper incisors (Merriam, 1895), and degree of hypsodonty, presence of roots on cheekteeth, and development of dentine tracts on sides of cheekteeth (Hibbard, 1950, 1967).

Parapliosaccomys is known from the Barstovian land mammal age (Lindsay, 1972; Korth, 1990), through the Clarendonian and Hemphillian (Shotwell, 1967), and thus occurs earlier in the fossil record than any geomyid other than *Dikkomys*. *Parapliosaccomys* has asulcate upper incisors, hypsodont cheekteeth (strongly so in advanced species), reduced roots on premolars, and roots probably absent from molars of advanced taxa (Korth, 1987), and moderately to well developed dentine tracts.

Pliosaccomys, Clarendonian to early Hemphillian, may overlap *Parapliosaccomys* in time but the dentition differs from that genus, though it too lacks grooves on the upper incisors. The cheekteeth are only moderately hypsodont, roots are well developed on molars, and strong and divergent on premolars. Dentine tracts are absent or, in rare instances, scarcely developed. The listed differences readily separate the two genera. However, hypsodonty, loss of roots on cheekteeth, and development of dentine tracts are partially independent but interrelated characters that have evolved several times in other geomyoids (Entoptychidae—Rensberger, 1971; Dipodomyinae—Dalquest and Carpenter, 1986, for example). Strong roots of cheekteeth, divergent in the upper teeth of primitive geomyids such as *Pliosaccomys*, interfere with the upward movement of the teeth in their alveoli to replace wear at the occlusal end. To permit free upward growth, roots are reduced in size, rotated to a position parallel with the tooth axis, and eventually lost. Sharpey's fibers, that hold teeth in their alveoli, do not penetrate the enamel of the tooth crown. Dentine tracts (where enamel is absent) form so that the connective tissue fibers may anchor a tooth to its alveolar wall (Dalquest and Carpenter, 1986).

Sulci on the upper incisors of modern pocket gopher genera are basic taxonomic characters. Merriam (1895) used five sulcus patterns to define genera (generic names in quotation marks in the following list are now considered subgenera or synonyms): asulcate or with a single tiny groove on the inner margin (*Thomomys*); unisulcate, with shallow groove median, or slightly on inner side (*Cratogeomys*, *"Platygeomys,"* *Pappogeomys*, *Orthogeomys*); unisulcate, with a deep groove well over on inner side (*"Macrogeomys," "Heterogeomys"*); bisulcate, with median groove on outer side of center of tooth (*Zygogeomys*); bisulcate, with narrow, deep groove on inner margin and shallow median groove near center or on inner side of incisor (*Geomys*). Incisor grooves of geomyids appeared between the early Hemphillian, when the last asulcate *Pliosaccomys* lived, and the early-late Hemphillian, when the shallowly bisulcate *Progeomys* lived. By the Blancan, sulci of *Geomys* were like those of modern species.

No Miocene geomyids thus far described seem to represent the unisulcate genera. *Cratogeomys*, at least, was in existence in essentially modern form in the early Blancan (Gidley, 1922).

Progeomys, of the mid- (or early late) Hemphillian (*ca.* 6.6 MYBP), has shallow bisulcate upper incisors, may be slightly more hypsodont than the latest species of *Pliosaccomys*, but has strong roots on cheek-teeth and lacks dentine tracts. It is intermediate between *Pliosaccomys* and *Geomys*. The youngest premolar of this genus available has the enamel cap worn away but still shows the Z-pattern.

Pliogeomys, of late Hemphillian age, is still further advanced in the *Geomys* line. The lower premolars figured by Hibbard (1954) are worn to the eight-pattern but obviously were originally quite hypsodont. Roots are well developed but not large. Dentine tracts are slender and probably did not extend more than half-way up the height of the crown. *Pliogeomys carranzai* is an advanced species (Lindsay and Jacobs, 1985) with extremely hypsodont teeth and small roots on the lower premolars. Dentine tracts extend approximately three-quarters of the height of the crown. Incisor grooves are of normal *Geomys* type. This species is nearly at the *Geomys* evolutionary level. The enamel cap pattern of P4 of *Pliogeomys* is unknown.

Nerterogeomys was proposed by Gazin (1942) for Blancan pocket gophers of the *Geomys* type. Hibbard (1950) considered *Nerterogeomys* a subgenus of *Geomys*, as did Russell (1968). The enamel cap pattern of P4 in specimens of *Geomys* cf. *minor*, early Blancan, of the Beck Ranch local fauna of Texas, is indistinguishable from that of modern *Geomys*.

The evolutionary sequence *Pliosaccomys-Progeomys-Pliogeomys-Geomys* is documented by specimens. Ancestry of *Thomomys* is not clear. Almost everyone who has dealt with pocket gopher evolution has emphasized the magnitude of the differences between *Thomomys* and the genera with grooved upper incisors. The differences in enamel cap pattern of p4 are at least as distinctive. No pre-Blancan specimens of *Thomomys* have been described and Blancan *Thomomys* are little different from modern specimens. *Pleisothomomys*, described by Gidley and Gazin (1933), is distinct in having oval rather than pear-shaped molars and in some other details. However, it seems confined to the Pleistocene of the eastern United States (Russell, 1968), and Blancan age *Thomomys* with typical, pear-shaped molars are known (Shotwell, 1967). Shotwell (1967) also figured a lightly worn P4 with a broad, deep labial re-entrant suggestive of modern *Thomomys*.

Thomomys might have descended from *Parapliosaccomys*, as was suggested by Shotwell (1967). Even Hemphillian *Parapliosaccomys* are not greatly different from *Thomomys*. Roots are strong but cheek-teeth are quite hypsodont and dentine tracts extend two-thirds of the height of the enamel. Slight increase in height of dentine tracts and loss of roots would bring *Parapliosaccomys* to the *Thomomys* evolutionary level.

Conclusions

Parapliosaccomys and *Pliosaccomys* share the Z-pattern that seems to be unique to geomyids, and both genera probably are descendant from the early Miocene *Dikkomys*. The modern *Thomomys*, with essentially asulcate upper incisors and nondenticulated crests on the enamel caps of the premolars, probably is descendant from *Parapliosaccomys* but intermediate taxa are undescribed. *Geomys*, with bisulcate upper incisors and strongly denticulated crests on the enamel cap of the premolars, is descendant from *Pliosaccomys*; *Progeomys* and *Pliogeomys* are intermediate steps in the evolution of modern genera. Enamel caps of Blancan *Geomys* do not vary appreciably from those of modern *Geomys bursarius*. The fossil record furnishes no evidence of the ancestry of the modern unisulcate genera, *Cratogeomys*, *Orthogeomys*, and the bisulcate *Zygogeomys*. Pertinent fossils eventually may be discovered in México or Central America.

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